A computational study of anticipation in the retina

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Introduction

Most models of the early visual system consider simple and decorrelated retino-thalamic entries. However, studies have shown the retina is able to perform complex tasks using for instance motion anticipation to compensate delays in retino-cortical transmission [1], [2]. There exists models of retina anticipation, based on gain control at the level of retinal ganglion cells (RGCs) and bipolar cells, able to reproduce several motion features. In this work, we propose an extended version of those models, implementing gain control, lateral connectivity via gap junctions, and sensitivity to orientation. We study the variability of temporal anticipation as a function of stimulus parameters with the gain control model. We then study the effect of ganglion cell connectivity through gap junctions on motion encoding, and conduct a similar analysis of anticipation variability. We finally extend the model in 2D and introduce an integration method of anisotropic Gaussians inspired from computer vision. We show that anisotropy can reduce shape artifacts introduced by gain control.

General context

The retina has two main layers, bipolar and ganglion cells. Those are connected either directly through the dendritic field or gap junctions, or indirectly through interneurons called amacrines. We want to understand which role is played by non-linear phenomena at the level of single cells as well as connectivity in motion processing and anticipation in particular.

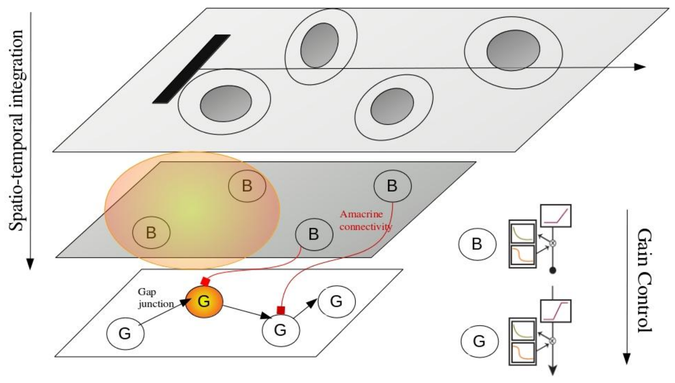

Figure 1: Schematic of the retinal mechanisms involved in motion processing.

Gain control model description

The cascade model used in this work, from Chen & al. [2], is able to reproduce several motion processing features such as anticipation, alert response to motion onset and motion reversal.

A visual stimulus $S(x, y, t)$ is first convolved with the spatio-temporal receptive field $K(x, y, t)$, followed by a non-linearity and a bipolar gain control function. Ganglion cells then pool the response of several bipolar cells with Gaussian weights and a second level of gain control is applied.

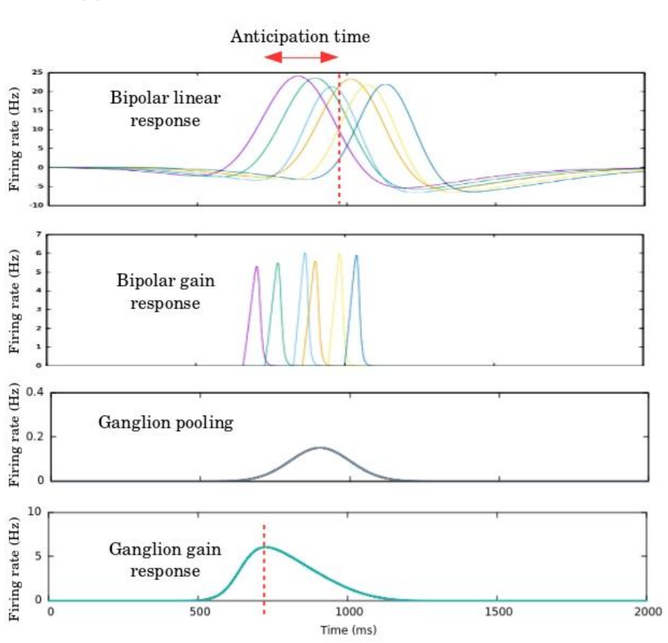

Figure 2: A shift in the response peak shows that ganglion cells are most sensitive to the bar before it reaches the center of their RF. We call time anticipation the lag between the peak of the average bipolar linear response and ganglion output.

Model variability

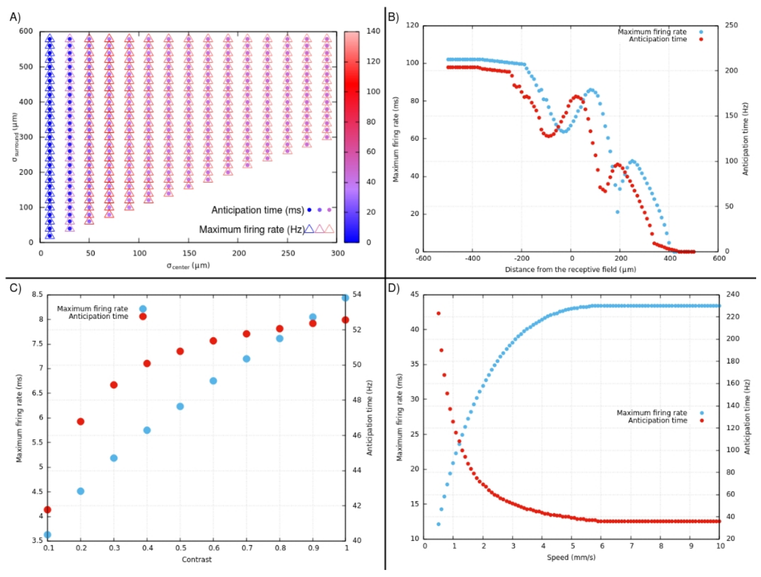

Figure 3: Variability of the model. A) Anticipation increases with the center std of the receptive field (RF), and is invariant with regards to the surround. B) Anticipation is maximum when the bar spans the whole RF and follows the RF variations. C) Anticipation increases with contrast and D) decreases with velocity. In all the subfigures, firing rate follows the anticipation except for velocity.

Gap junctions model description

Direction-selective ganglion cells along with parasol cells are involved in motion processing. They are connected through gap junctions, either at the bipolar or the ganglion level. Trenholm & al. [3] have shown that these gap junction play a role in lag normalization : cells respond to the leading edge of moving objects at a constant spatial location, regardless of their speed, in a certain velocity range. Ganglion cell activity is given by :

$$V_g^n(t) = V_b(t) + \alpha V_g^{n-1}(t)$$

where $V_g^{n-1}(t)$ is the activity of the downstream cell, in the direction of motion, $V_b(t)$ the bipolar input and α the strength of the gap junction.

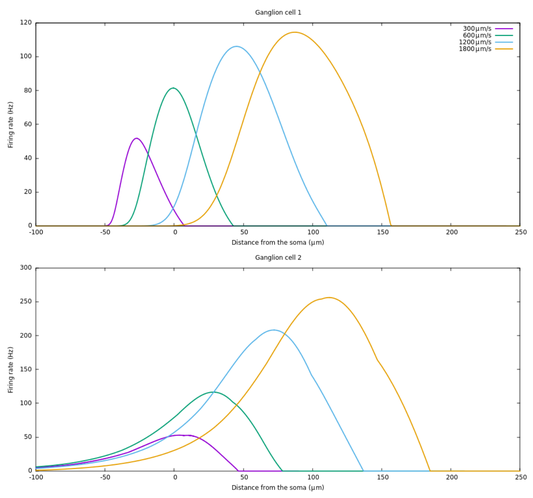

Figure 4: Lag normalization is developed by cells far from the start of motion. Different colors correspond to the stimulus velocity.The bar is 300 µm wide, and the distance between two cells is 75 µm.

This effect only appears when the stimulus is large enough to cover more than the receptive field of just one ganglion cell .

More than lag normalization, gap junctions are also accountable for motion anticipation. There are indeed two types of anticipation triggered by gap junctions : an earlier increase in activity and a slight shift in the peak response when α is large enough.

Model variability

We study here how time anticipation depends on the model's and the stimulus parameters. For consistency, we choose the same definition of time anticipation as in gain control. As in the gain model, anticipation decreases for large values of velocities which could be seen as an intuitive physical constraint to anticipation.

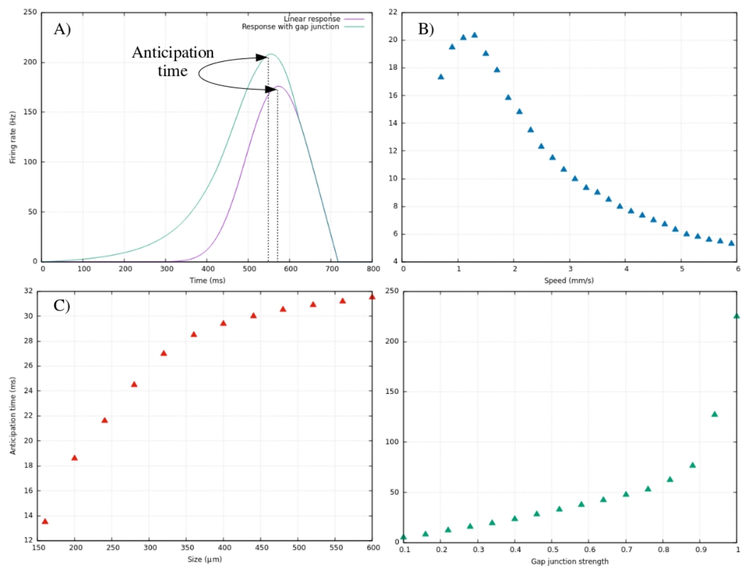

Figure 5: Variability of the model. A) Definition of anticipation time B) Anticipation decreases overall with velocity. C) Anticipation increases with the size of the bar and D) with the strength of gap junctions.

Anisotropy

Recent studies [3] have shown that some retinal neurons are tuned to the orientation of elongated visual stimuli. We implement anisotropic filtering by using the equivalence found by Geusenroek & al [4]: the Gaussian of std σ_u and σ_v and rotation angle θ can be rewritten in a non orthogonal system of axes (x,ϕ).

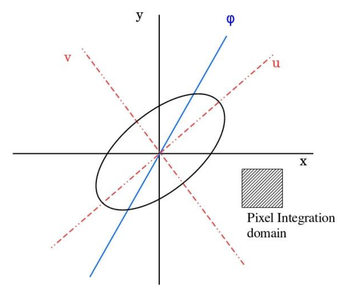

Figure 6: Filter transformation. The dashed square represents the integration domain, its boundaries are written in the new system of axes.

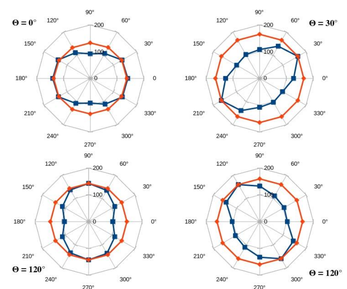

Figure 7: Tuning curves of bipolar cells show that the peak response of the cell occurs when the bar in the preferred orientation.

Anticipation and shape

Within the isotropic framework, when the receptive field is smaller than the bar's size, gain control produces shape deformation. This can be reduced through anisotropy.

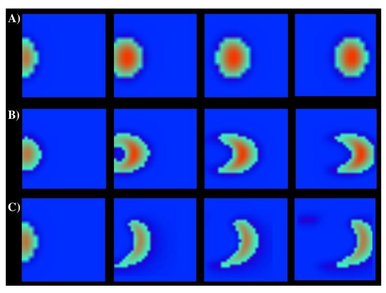

Figure 8: Anisotropy reduces shape deformation. A) Linear response of bipolar cells. B) The response of the gain control model. C) Same as B) with anisotropic cells in the upper half of the square response.

Conclusion

We studied two retinal mechanisms involved in motion processing : gain control and gap junction connectivity between ganglion cells. We emphasized the effect of the models' parameters alongside the stimulus properties on the ability of the models to anticipate smooth motion. Parameters such as the stimulus speed, contrast and size seem to play a crucial role in anticipation, which should be further assessed through experiments. This work opens up perspectives of using the integrated model to study how anticipation works in the case of complex trajectories and to understand more thoroughly the effect of anticipation on the shape of the object. We would also like study other types of connectivity such as gap junctions at the level of bipolar cells and the one induced by amacrine cells.

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